A STUDY OF RECIPROCAL HYBRIDS IN PAPAYA

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INTRODUCTION

The papaya, Carica papaya L., is a well known edible fruit throughout the tropics. It has long been an important commercial fruit crop in the Hawaiian Islands. In the monograph of the Caricaceae, Harms (1925) stated that all 40 species of the genus Carica are dioecious, except that hermaphrodite forms exist in C. papaya. Solo, the commercial papaya variety in Hawaii, has both hermaphrodite and female sex forms. The hermaphrodite is more desirable to the grower, not only because every tree produces fruit, but also because consumers prefer the pyriform fruit of the hermaphrodite to the spherical female fruits.

One of the problems confronting papaya growers in Hawaii is the inability to distinguish the sex of young seedling plants. At present, the sex type of papaya plants can be determined only from the flowers, which appear six months or more after seed germination. Although seeds of selfed hermaphrodite produce only two hermaphrodites to one female (Hofmeyr, 1938), growers consider this ratio to be an economic detriment in orchard plantings. It is, therefore, usual to transplant seedlings in groups of two or three, and thin to one when sex is determined. The inefficiency of this procedure has compelled investigators in many papaya growing countries to seek ways to distinguish between sexes at an early seedling stage.

Studies of reciprocal hybrids of properly selected parents could be useful in locating sex-linked characters, some of which might be useful in the early separation of the sexes. Unfortunately, in the absence of good qualitative characters, only quantitative ones were available for investigation.

Characters studied in this problem were: terminal height, stem diameter, height to first flower, number of nodes to first flower, internode length and earliness of flowering.

REVIEW OF LITERATURE

Literature pertaining to this problem is discussed under the following headings: (1) sex determination, (2) qualitative inheritance, and (3) quantitative inheritance.

Sex Determination

The three basic sex forms in papaya and their variant forms, as complicated by cyclic changes in fertility, are often not well understood and this has led to a number of conflicting interpretations and discussions of the sex situation in papaya. Storey (1938b) and Hofmeyr (1938) reported independently on genetical studies of sex determination in papaya and came to similar conclusions. Sex in papaya is controlled by three allelomorphic factors:

M1 = dominant factor for maleness

M2 = dominant factor for hermaphroditism

m = recessive factor for femaleness

Phenotypic effects:

M1m = the male or staminate plant

M2m = the hermaphrodite plant

mm = the female or pistillate plant

The dominant combinations, M1M1, M2M2, M1M2, were found to be zygotically lethal as a result of retarded development of endosperm and embryo in papaya seed (Lamoureux, 1955).

A belief among papaya growers that plants of one sex or the other grow faster in the young seedling stage has encouraged workers in several countries to seek ways of separating the sexes at an early seedling stage. External appearance of the seed, its location within the fruit, general phenotype of young plants, and certain specific seedling characteristics were tested by Sakurai (1929). None of these characters proved to be of positive value in predicting the sex of plants.

Elden (1935), Hofmeyr (1938), Pope (1930), and Reyes (1925) also investigated several methods proposed to separate the sexes on the basis of young seedling characteristics, none of the methods were successful.

Kumar (1951), in a preliminary study of growth rates of papaya seedlings prior to flowering, found that male seedlings 12 weeks old had a higher rate of stem elongation than female or hermaphrodite seedlings. However, he did not find differences in growth between female and hermaphrodite plants. He suggested further studies before definite conclusions could be drawn.

Sakurai (1929), Hofmeyr (1938), and Nakasone (1952) all conducted progeny tests and reported failure to detect differences in growth between plants of different sexes prior to flowering. Sakurai and Hofmeyr both used height of stem at a given age as growth index, while Nakasone measured and studied earliness of flowering, height to first flower, and number of nodes to first flower.

A recent study on growth inheritance of two Solo papaya strains by Hamilton (1954) has shown differences in growth rate between female and hermaphrodite plants. The differences involved were, however, relatively small and probably would not provide a practical means of determining the sex of plants prior to flowering.

Qualitative Inheritance

Storey (1953) listed several qualitative characters inherited as autosomals, and three sex-linked characters. These are: (1) yellow flower color, Y, dominant to white; (2) purple stem and petiole, P, dominant to green (Hofmeyr, 1938); and grey seed coat, S, dominant to black (Hofmeyr, 1941b).

Mutant genes in papaya have been studied extensively by various workers in an attempt to find sex-linked vegetative characters which might be useful in early separation of plants of different sexes. Hofmeyr (1941a) found that Y and P are sex-linked with the following approximate relationship: M1 25 Y 16 p. Storey (1953), using material given him by Hofmeyr, came out with similar values. Unfortunately, the linkage between sex and color of flower is not of practical value because flowers cannot be examined prior to flowering. The linkage between sex and stem color has little practical value in sex determination because of the high percentage of crossing-over (41%) between these characters.

In another report, Hofmeyr (1941b) found that the crossing-over percentage of the seed coat sex-linked character is 31.1 $\pm$ 4.5. Its gene position in relation to the other genes on the sex chromosome has not been determined, and it would be of little practical value in sex determination because of the high percentage of crossing-over.

Quantitative Inheritance

Hofmeyr (1938) concluded from his studies of growth rate in papaya that either diameter or height of stem was a reliable index of plant

vigor, when these measurements were taken at or before plants began to set heavy crops of fruit.

Storey (1943) reported on a study dealing with the inheritance of fruiting height in reciprocal crosses between relatively high-fruiting inbred Solo strains and four different low-bearing foreign accessions. He concluded that multiple factors were involved in the inheritance of height of bearing and that the product of any cross was intermediate to and closely approaching the arithmetic mean of the parental types.

Nakasone (1952) carried out progeny tests to determine the mode of inheritance of the characters height to first flower, earliness of flowering, number of nodes to first flower, and internode length. Crosses were made between male and female plants from the Betty papaya, an early fruiting semi-dwarf type, and hermaphrodite and female plants from Line 5 Solo, a tall, late fruiting strain. He found the F_1 means of all characters studied to be intermediate to the two parents. The F_1 means for the characters height to first flower and number of nodes to first flower were found to deviate from the mid-point of the two parents in the direction of the short parental Betty variety, suggesting geometric effects or interaction by non-allelic genes. Partial dominance from the short parent was also suggested as a possible explanation. No evidence of heterosis or complete dominance was found in the F_1, and no loss of vigor was detected in comparing the F_1 with the F_2.

The mode of inheritance reported by Storey (1943) and Nakasone (1952) is common in nature and commonly referred to by geneticists as quantitative inheritance. These characters, as defined by Smith (1944),

relate to measurable differences in degree rather than in kind, and normally exhibit a continuous range of variability in segregating populations.

The study of means is a valuable tool in the interpretation of quantitative inheritance data. Powers (1941) postulated a hypothesis to evaluate means of such data: the F_1 means are to be compared with the parental means to obtain information as to whether heterosis, complete dominance, partial dominance, or no dominance exists.

MATERIALS AND METHODS

Materials

The materials used in this study were two highly inbred strains of Solo papaya, and their reciprocal hybrids. The parental types were (1) Line 8: yellow fleshed with low carpellody, flowering four to six months from seed at from 55 to 70 inches from the ground, and (2) Line 9: pink fleshed with slightly more carpellody than Line 8, flowering within three to five months from seed at from 30 to 45 inches from the ground. Both strains have been maintained by selfing perfect flowers on hermaphrodite plants for at least six consecutive generations. The reciprocal hybrids obtained from (1) Line 9 female pollinated by Line 8 hermaphrodite, (2) Line 8 female pollinated by Line 9 hermaphrodite.

The parental types and their reciprocal hybrids are listed below:

Treatment	Progenies	Type Designation
1	Line 8 ♂ ⊗	P1 (Parental)
2	Line 9 ♂ ⊗	P2 (Parental)
3	Line 9 ♀ x Line 8 ♂	H1 (Hybrid)
4	Line 8 ♀ x Line 9 ♂	H2 (Hybrid)

Seed Individual flowers from each of the parental plants were self- and cross-pollinated as shown above.

Seedlings Seedlings of the four seed lots were grown from seeds planted directly in 20-ounce cans on January 22, 1960. The seedlings were uniform in size and appearance at the time of transplanting into the field.

Field Planting

The field planting was made in the University Farm on June 10, 1960. At transplanting time the plants were about 20 centimeters in height with six to eight true leaves.

The plants were set out in randomized complete blocks with 20 replications. This resulted in a field planting of five rows of 16 groups of two plants each with border rows on all four sides of the field. Plots were randomized within blocks. Plants were spaced 7 feet apart in rows 8 feet apart. Figure 1, taken diagonally across the field from the upper end at which time two plants remained at each place, and Figure 2, taken parallel to the row, after thinning to a single plant, show the relative uniformity of spacing between rows and between plants in the row. No serious cultural difficulties were encountered in growing the plants except for the loss of few plants at transplanting and a single virus infected plant in one border row.

FIG. 1. Diagonal view of field planting at two months after transplanting, showing irrigation furrows and uniform spacing of plants in rows.

FIG. 2. View of field planting taken parallel to rows at five months after transplanting.

Culture. The field was furrow irrigated along the rows, twice a week. Weeds were controlled by hand hoeing when plants were small and by spraying with activated diesel oil emulsion after they were over five months old. Fertilizers were applied at monthly intervals.

Methods of Taking Data

Data were taken on the following characters:

1. Terminal height
2. Stem diameter
3. Height to first flower
4. Number of nodes to first flower
5. Internode length
6. Earliness of flowering

A paint mark was placed on the stem 10 cm. above the cotyledonary node for accurate and easy measurement of data.

Terminal Height was the measurement of the stem between the paint mark and the terminal growing point three months after transplanting. At this time many of the plants had begun to flower.

Stem Diameter. Measurements were taken at the same time as data on height to terminal growing point. The stem circumference was measured at the paint mark and diameter computed to centimeters with two decimal points by dividing by 3.1416. This method assumes the stems to be round, which they essentially are.

Height to First Flower was taken as the number of centimeters between the paint mark and the first flower.

Number of Nodes to First Flower was the number of nodes between the paint mark on the stem to the node at which the first flower appeared.

Internode Length Data on this character were calculated by dividing the height to first flower by the number of nodes to first flower.

Earliness of Flowering This was the number of days from transplanting date to first flower opening.

Method of Analysis

The experimental planting was made in complete randomized blocks. The data used were the average of the two plants in each treatment. This procedure is justified by the fact that in all characters studied, no significant difference was found between data from female and hermaphrodite plants growing in the same hill.

The statistical methods followed in analysis of data are given in Snedecor (1959). In the analysis of variance, the appropriate error for comparing progenies and blocks is that within progenies. In the test of differences between progeny means, multiple range and multiple F tests (Duncan, 1955) were employed.

In testing the significance of the difference between means of the reciprocal hybrids and the mid-point of the two parental lines, the following formula as given by Paterson (1939) was employed:
$SE_D = \sqrt{SE_A^2 + SE_B^2}$ and $t = \frac{D}{SE_D}$, where SE_D is the standard error of the difference between means. A significant difference is one that gives a greater calculated value of t than the corresponding value from the t table at the 5 or 1 per cent level.

EXPERIMENTAL RESULTS

Terminal Height

The character, terminal height, is the portion of the stem from a point mark, 10 cm. above cotyledonary node to the terminal growing point, measured to the nearest half centimeter at three months after transplanting.

Analysis of variance for terminal height is shown in Table Ia.

TABLE Ia. ANALYSIS OF VARIANCE FOR MEAN TERMINAL HEIGHT IN CENTIMETERS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F.	F.05	F.01
Total	79	11,516.94				
Progenies	3	3,428.88	1,142.96	13.81**	2.78	4.16
Blocks	19	3,371.78	177.46	2.14*	1.76	2.23
Error	57	4,716.28				

Coefficient of variation (C) = 11.12%

Differences in block means were found to be significant at the 5 per cent level, suggesting differences due to environmental influences. Differences between progenies were highly significant. The test for mean differences shown in Table Ib indicated that the mean height to terminal growing point of P2 (short parent) differed significantly from the means of P1 (tall parent) and H2 but not from H1. Differences were not detected among the means of H1, H2 and P1.

TABLE Ib. MEAN TERMINAL HEIGHT IN CENTIMETERS

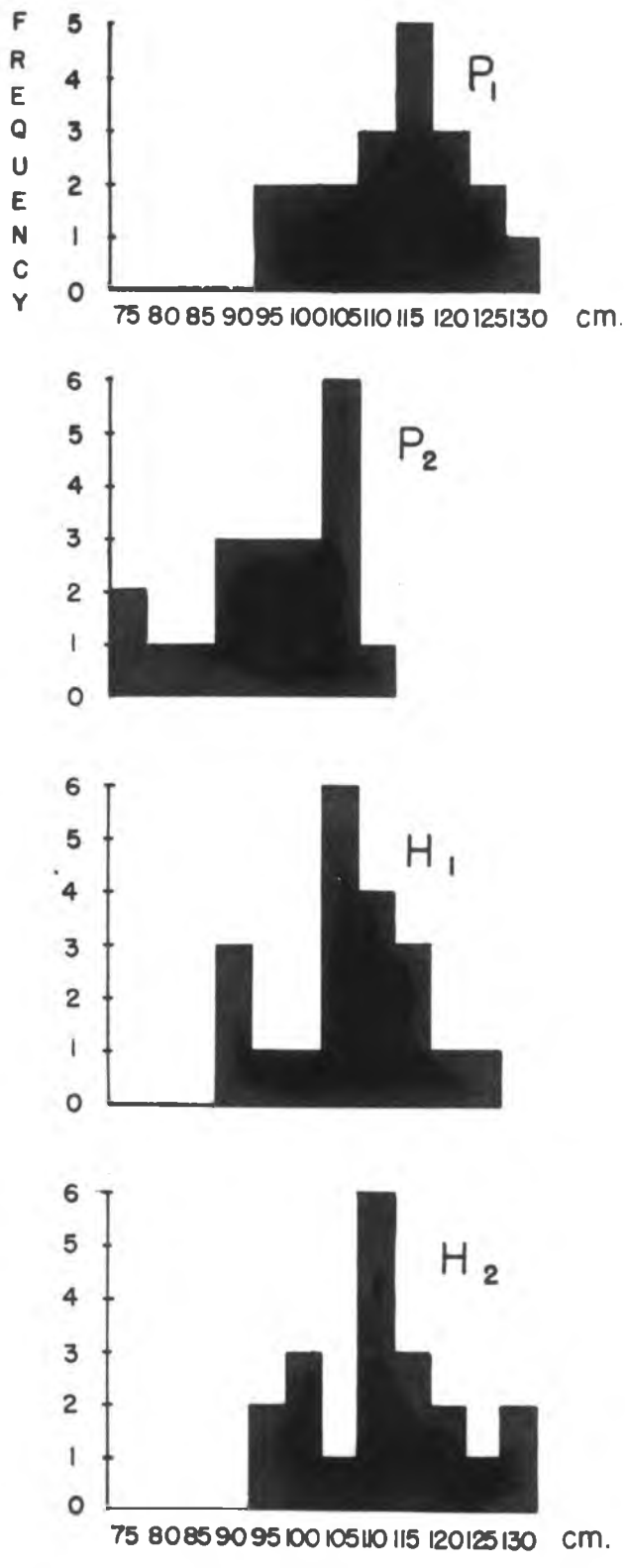
Progenies:	P2	H1	H2	P1
Means :	97.8	108.8	113.5	114.2

Note: Any two means not underscored by the same line are significantly different. Any two means underscored by the same line are not significantly different.

The H1 and H2 progeny means do not differ significantly from 106.0 cm., the mid-point of the two parental lines, or from 114.2 cm., the P1 mean. However, the average of the two hybrid progenies, 111.1 cm. is nearer the P1 mean of 114.2 cm. than 106.0 cm., the P1 and P2 mid-point. Also, the H2 and P1 means are equal when rounded off to the whole centimeter, which is at least suggestive of dominance. The difference between P1 and P2 is only 16.4 cm. and the ranges of all four progenies as shown in Fig. 3 overlap. With the numbers of plants involved the test for dominance or lack of dominance is inconclusive. It would probably require additional testing with larger numbers of plants to provide conclusive evidence of type of inheritance involved in mean height to terminal height.

TABLE Ia. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR TERMINAL HEIGHT

Progenies	$\bar{X} \pm$ S.E. (cm.)	Variance	St. Dev.	C = %
P1	114.2 ± 4.96	99.19	9.96	8.72
P2	97.8 ± 6.03	120.53	10.98	11.22
H1	108.9 ± 4.91	98.15	9.91	9.11
H2	113.5 ± 5.39	107.82	10.38	9.15



TERMINAL HEIGHT

Stem Diameter

The character, stem diameter, is the thickness in centimeter of the stem at a reference point 10 cm. above the cotyledonary node at a given time three months from transplanting. The measurements were computed from the circumferences. Sex differences were also tested but there appeared to be no significant differences due to sex.

TABLE IIa. ANALYSIS OF VARIANCE FOR MEAN STEM DIAMETER IN CENTIMETERS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F.	F.05	F.01
Total	79	49.85				
Progenies	3	2.15	0.72	1.95	2.78	4.16
Blocks	19	26.71	1.41	3.82**	1.76	2.23
Error	57	20.99	0.37			

C = 12.17%

Analysis of variance for this character showed the blocks to be significantly different, but failed to indicate significant differences between progenies, suggesting that stem diameter was influenced to a greater degree by environmental conditions than by inherited factors.

The pertinent statistics for this character are presented in Table IIb. The difference in stem diameter of P1 and P2 was 0.20 cm. with the estimated arithmetic mean of the parental lines at 6.40 cm. The H1 mean fell on the mid-point of the parents and the H2 mean was slightly but not significantly larger than the P1 and P2 means.

TABLE IIb. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR STEM DIAMETER

Progenies	$\bar{X} \pm$ S.E. (cm.)	Variance	St. Dev.	C = %
P1	6.30 ± 0.028	0.567	0.75	11.95
P2	6.50 ± 0.022	0.438	0.66	10.18
H1	6.40 ± 0.040	0.798	0.89	13.97
H2	6.74 ± 0.035	0.707	0.84	12.48

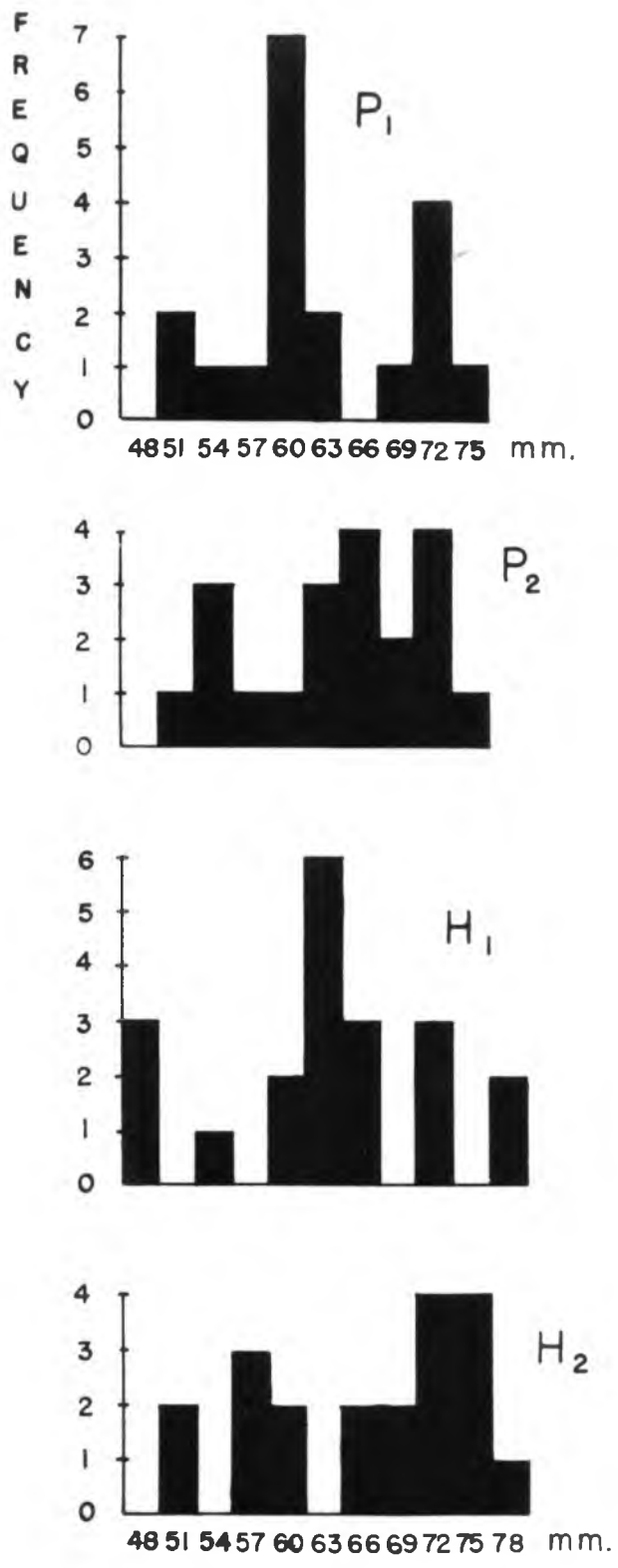
Frequency histograms for the distribution of stem diameters are presented in Fig. 4. The ranges of the two parents and their reciprocal hybrids were relatively wide and overlapping.

Height to First Flower

The character, height to first flower, is the portion of stem from a paint mark, 10 cm. above cotyledonary node, to the first flower leaf-axil, measured to the nearest half-centimeter at the time of first flower opening.

Differences due to sex of plant were tested and failed to show significance. The method of analysis followed was the same as for other characters. Table IIIa shows the analysis of variance for height to first flower.

Analysis of variance for this character failed to indicate significant differences between blocks suggesting relatively uniform environmental conditions. Progenies, on the other hand, gave a highly significant F value.



STEM DIAMETER

TABLE IIIa. ANALYSIS OF VARIANCE FOR MEAN HEIGHT TO FIRST FLOWER IN CENTIMETERS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F.	F.05	F.01
Total	79	83,852.59				
Progenies	3	76,420.79	25,473.60	257.18**	2.78	4.16
Blocks	19	1,785.86	93.99	0.95	1.76	2.23
Error	57	5,645.94	99.05			

C = 29.94%

As shown in Table IIIb, mean height to first flower in the two parents and their reciprocal hybrids showed significant differences at the 5 per cent level. No difference was detected between the two hybrids, suggesting that cytoplasmic and sex-linked inheritences probably did not influence this character.

TABLE IIIb. MEAN HEIGHT TO FIRST FLOWER IN CENTIMETERS

Progenies:	P2	H2	H1	P1
Means:	62.2	110.6	111.3	150.5

Table IIIc gives pertinent statistics for mean height to first flower. The difference in height to first flower between P1 and P2 was 88.3 cm. which is significant at the 1 per cent level. The mid-point of the parental lines was 106.4 cm. The H1 and H2 means deviated slightly but not significantly from this mid-point towards the mean of P1. This suggests that dominance was not involved but that probably multiple factors with additive effects influenced bearing height. The presence of interaction between non-allelic genes affecting this character is also considered a possibility.

TABLE IIIc. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR HEIGHT TO FIRST FLOWER

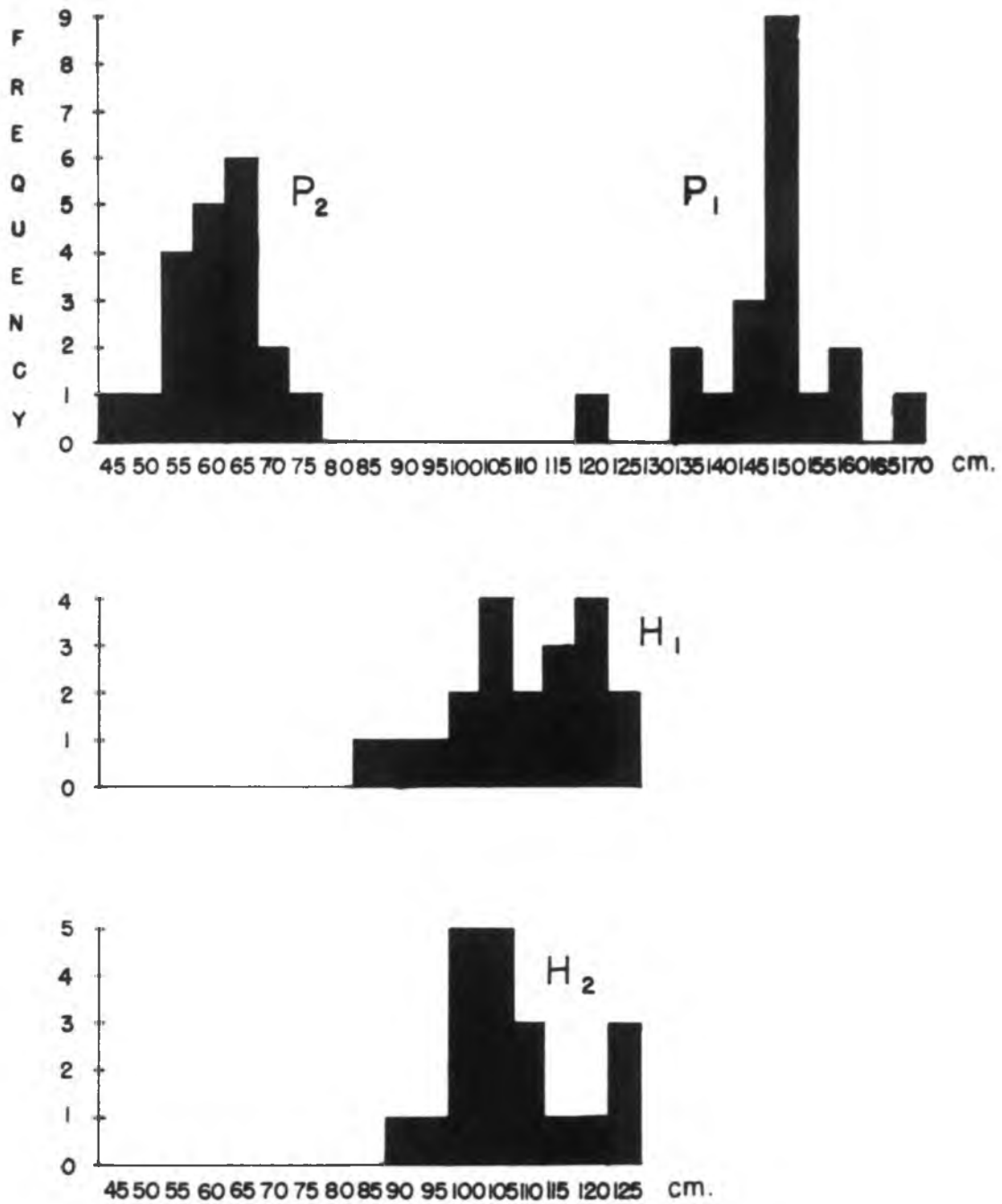
Progenies	$\bar{X} \pm$ S.E. (cm.)	Variance	St. Dev.	C = %
P1	150.5 ± 5.26	103.2	10.3	6.8
P2	62.2 ± 2.71	54.3	7.4	11.9
H1	111.3 ± 6.21	124.2	11.1	10.0
H2	110.6 ± 4.98	99.7	10.0	9.0

The range of distribution of the parental lines and their reciprocal hybrids, shown in Fig. 5, was relatively narrow. This could be expected from highly inbred lines and non-segregating progenies which should be relatively homozygous and therefore affected primarily by environmental factors. Ranges of P1 and P2 progenies were readily separable for this character, showing a clear-cut distribution between parental lines. The ranges of distribution for both hybrids fell between the ranges of the two parents, and were skewed in the direction of the P1 distribution.

Number of Nodes to First Flower

The number of nodes to first flower is the actual count of nodes from the paint mark on the stem to the node at which the first flower appeared. As in other characters mentioned previously, there was no evidence of differences due to sex of plant for this character.

Analysis of variance for number of nodes to first flower is given in Table IVa. Highly significant differences are suggested for blocks as well as progenies, indicating that number of nodes to first flower has probably been affected by environmental conditions.



HEIGHT TO FIRST FLOWER

TABLE IVa. ANALYSIS OF VARIANCE FOR MEAN NUMBER OF NODES TO FIRST FLOWER

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F.	F.05	F.01
Total	79	3,944.60				
Progenies	3	3,342.46	1,114.15	196.50**	2.78	4.16
Blocks	19	278.91	14.68	2.58**	1.76	2.23
Error	57	323.23	5.67			

C = 23.93%

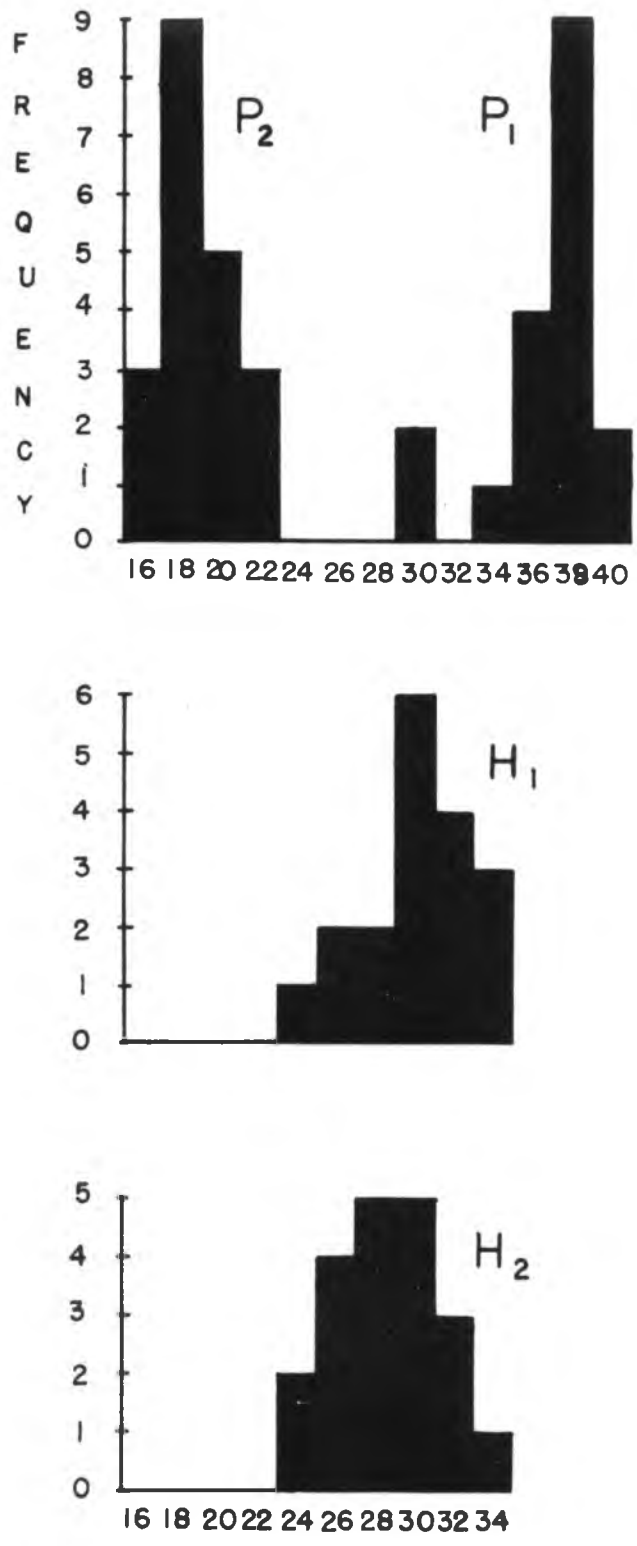
The mean number of nodes to first flower of the two parents and their reciprocal hybrids are given in Table IVb. These showed significant differences at the 5 per cent level. The two hybrids appeared similar in number of nodes to first flower, indicating that probably neither cytoplasmic inheritance nor sex-linkage was involved.

TABLE IVb. MEAN NUMBER OF NODES TO FIRST FLOWER

Progenies:	P2	H2	H1	P1
Means:	19.6	29.2	31.7	37.6

As shown in Table IVc, the difference in number of nodes to first flower between P1 and P2 was 18.0 with the mid-point of the two parents at 28.6. Deviations of the H1 and H2 means from this mid-point were in the direction of the tall parent, but were not significant at the 5 per cent level.

Frequency histograms for the distribution of the number of nodes to first flower are presented in Fig. 6. The range of H1 and H2 fell in


FREQUENCY
9
8
7
6
5
4
3
2
1
0
P2
P1
16 18 20 22 24 26 28 30 32 34 36 38 40
6
5
4
3
2
1
0
H1
5
4
3
2
1
0
H2
16 18 20 22 24 26 28 30 32 34
NUMBER OF NODES

between the range of their parents and were slightly skewed in the direction of F1.

TABLE IVc. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR NUMBER OF NODES TO FIRST FLOWER

Progenies	$\bar{X} \pm$ S.E. (cm.)	Variance	St. Dev.	C = %
P1	37.6 ± 0.44	8.90	2.98	7.93
P2	19.6 ± 0.16	3.24	1.80	9.18
H1	31.7 ± 0.64	12.75	3.57	11.26
H2	29.2 ± 0.34	6.80	2.61	8.94

Length of Internodes

This character was calculated for each plant by dividing the height to first flower by the number of nodes to first flower. This ratio is an approximation of the mean internode length. The direct measurement of internode length was not considered practical. During the periods of optimum growth conditions, internodes are longer, while during the periods of poor growth conditions, internode lengths are considerably shortened. Another factor contributing to variation in internode length is the growth of plant at different stages. Younger, smaller plants have relatively shorter internodes than older, larger plants.

Differences due to sex of plant were also tested for this character, but were found not to be significant.

Analysis of variance for this character showed no evidence of block differences, but as in other characters studied, there were significant

differences between progenies. The relatively low coefficient of variation of 10.77 per cent suggests that for this character response of the four progenies to environmental conditions was relatively uniform.

TABLE Va. ANALYSIS OF VARIANCE TABLE FOR MEAN INTERNODE LENGTH IN CENTIMETERS

Source of Variation	Degrees of Freedom	Sum of Squares	Square	F.	F.05	F.01
Total	79	11.88				
Progenies	3	3.45	1.15	10.85**	2.78	4.16
Blocks	19	2.36	0.12	1.17	1.76	2.23
Error	57	6.07	0.11			

C = 10.77%

The only difference detected was between P1 and P2 (Table Vb). There was no evidence of differences between the two hybrids, and it is therefore assumed that the inheritance of this character was not cytoplasmic or sex-linked.

TABLE Vb. MEAN LENGTH OF INTERNODE IN CENTIMETERS

Progenies:	P2	H1	H2	P1
Means:	3.22	3.55	3.70	3.96

Table Vc shows pertinent statistics for mean length of internode.

As shown in Table Vc, the difference in internode length between P1 and P2 was 0.74 cm. with the mid-point of the two parents at 3.59 cm. The H1 and H2 means were found to be intermediate, closely approaching the arithmetic mean of the parental lines.

TABLE Vc. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR INTERNODE LENGTH

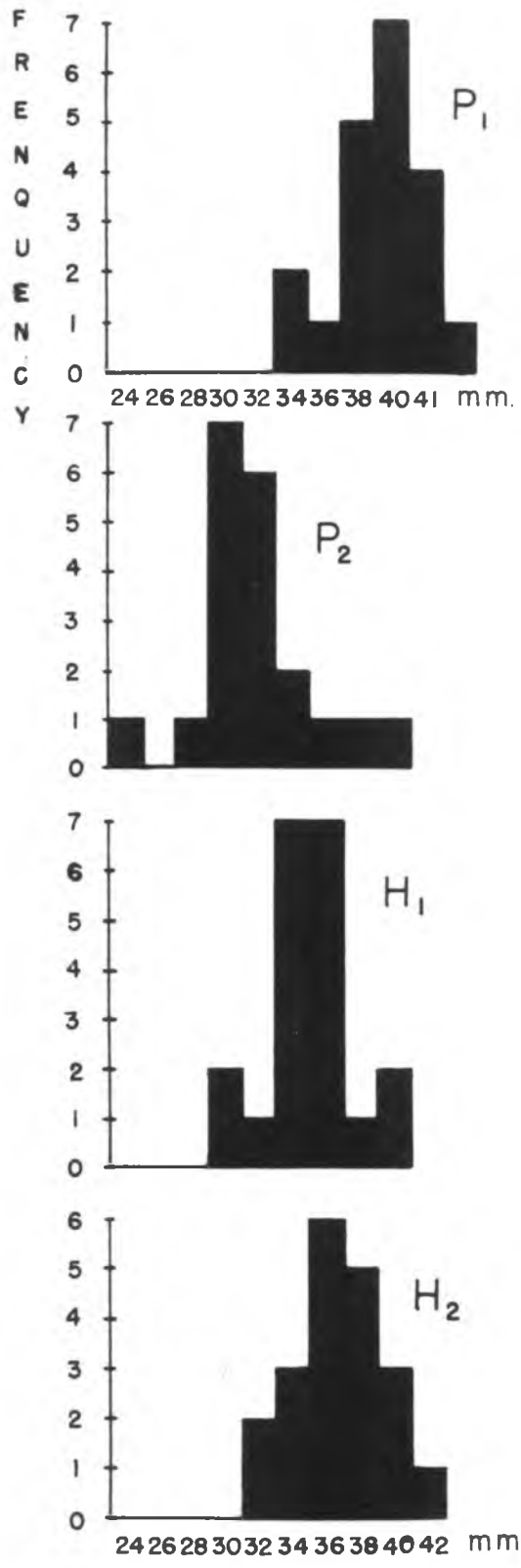
Progenies	$\bar{X} \pm$ S.E. (cm.)	Variance	St. Dev.	C = %
P1	3.96 $\pm$ 0.003	0.069	0.26	6.62
P2	3.22 $\pm$ 0.006	0.111	0.33	10.31
H1	3.55 $\pm$ 0.002	0.046	0.22	6.06
H2	3.70 $\pm$ 0.004	0.071	0.27	7.22

Frequency histograms for distribution of internode length are presented in Fig. 7. As in previous characters, the range of distribution of the parental lines and their reciprocal hybrids appeared to be relatively uniform. The ranges of H1 and H2 progenies were between the ranges of the parental lines, closely approaching their arithmetic mean.

Earliness of Flowering

The character, earliness of flowering, is the time in days from transplanting (June 10, 1960) to the day of first flower opening.

Differences attributable to sex of plant were not apparent in comparing the means of female and hermaphrodite plants at the same planting space. Analysis of variance for this character is given in Table VIa. There is no evidence of block differences, but as in other characters studied, there were highly significant differences between progenies.



LENGTH OF INTERNODES

TABLE VIa. ANALYSIS OF VARIANCE TABLE FOR MEAN TIME IN DAYS TO FIRST FLOWER OPENING

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F.	F.05	F.01
Total	79	19,386.25				
Progenies	3	15,097.36	5,032.45	95.40**	2.78	4.16
Blocks	19	1,270.19	66.85	1.26	1.76	2.23
Error	57	3,018.70	52.96			

C = 14.47%

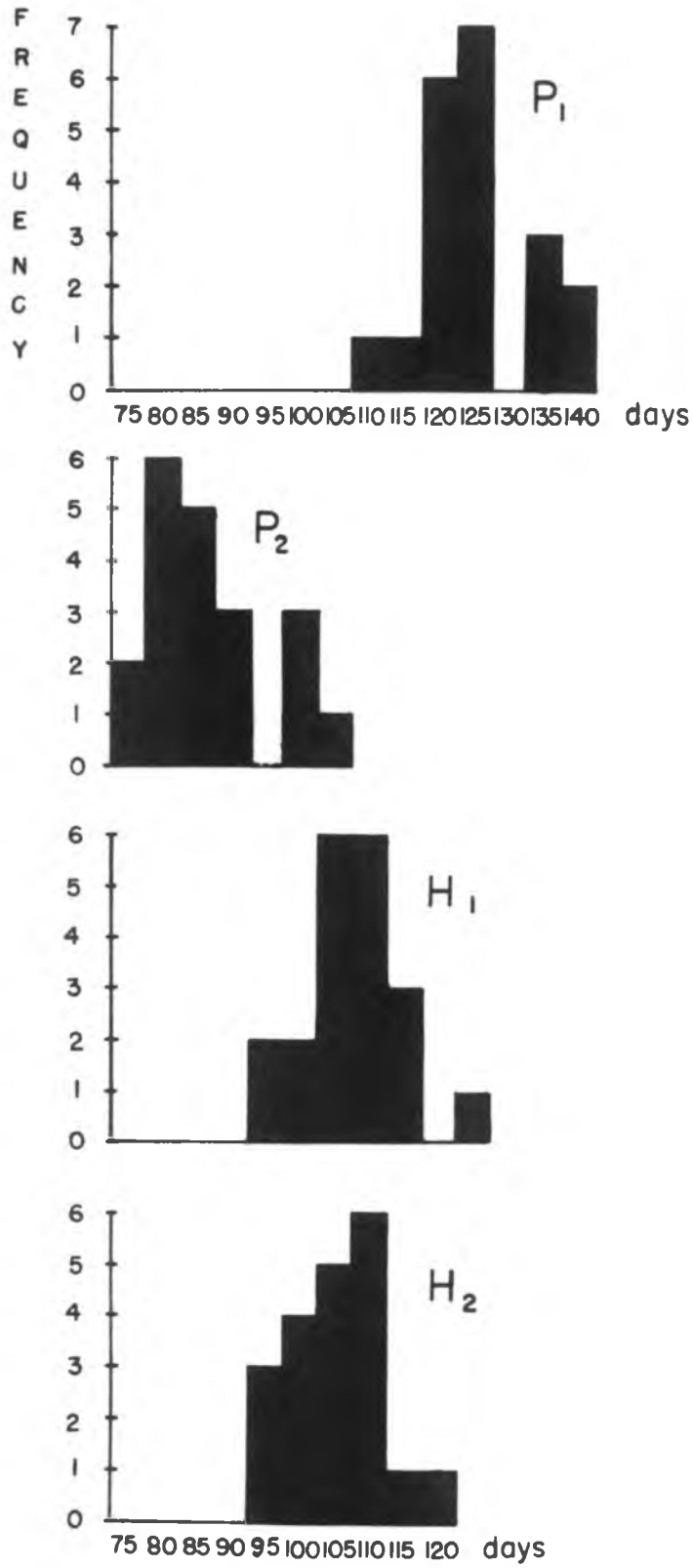
The mean time to first flower opening of the parents and their reciprocal hybrids showed significant differences at the 5 per cent level. Difference could not be detected between the reciprocal hybrids, suggesting lack of maternal influence or sex-linkage in this character.

TABLE VIb. MEAN TIME IN DAYS TO FIRST FLOWER OPENING

Progenies:	P2	H2	H1	P1
Means:	88.7	107.4	109.8	127.4

The difference between P1 and P2 in days to first flower opening was 38.7 with a mid-point of 108.0 days. The means of H1 and H2 were found to fall near the mid-point of the parental lines. The deviations were not significant at the 3 per cent level. This suggests lack of dominance in the inheritance of this character.

Frequency histograms for the distribution of earliness of flowering in the four progenies are presented in Fig. 8. The range of distribution of parental lines and their reciprocal hybrids was again



DAYS TO FLOWERING

relatively uniform and narrow. Ranges of H1 and H2 fall between that of the parental lines, closely approaching their arithmetic mean.

TABLE VIc. MEANS, STANDARD ERROR, VARIANCE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR EARLINESS OF FLOWERING

Progenies	$\bar{X} \pm$ S.E. (days)	Variance	St. Dev.	C = %
P1	127.4 ± 2.75	55.05	7.42	5.82
P2	88.7 ± 3.70	73.90	8.60	9.69
H1	107.4 ± 2.90	58.09	7.62	7.10
H2	108.8 ± 2.46	49.21	7.01	6.38

DISCUSSION AND CONCLUSIONS

It is evident that all the six characters studied exhibited a continuous range of variability as might be expected of quantitative characters. The distribution of means of the four progenies were of practical value in the interpretation of data and appeared to conform closely to the hypothesis proposed by Powers (1941).

In all characters studied, with the exception of terminal height and stem diameter, the means of the reciprocal hybrids were found to be approximately intermediate to the parental lines. There was no evidence of heterosis. Deviations of the hybrid means from the mid-point of the parental lines were not significant at the 5 per cent level. This suggests that multiple factors with additive effects may have been involved in all characters other than terminal height and stem diameter. The presence of interaction between non-allelic genes upon the same character is also considered as a possibility.

In all characters studied except earliness of flowering, the deviation of means of the hybrid progenies from the mid-point of the parental lines, though not significant, was always in the direction of the tall parent.

Studies of standard deviation of means of the four progenies were of some value as they exhibited uniformity in all the six characters studied. This is indicative of uniform genetic material as well as uniform experimental conditions. This is further verified by the relatively low coefficients of variation based on the means of the individual progenies.

It is interesting to note that the C value of P2 is slightly higher than that of P1 in five of the six characters. This suggests the possibility that the P1 parental line may be slightly more homozygous than the P2. If this is the case, it may be explained by the fact that P1 has been inbred for more generations than P2. The coefficients of variation of H1 and H2 were approximately of the same magnitude as to be expected in case of the hybrids of parents of similar genetic constitution.

As shown in the frequency histograms for all characters except stem diameter, the range of the four progenies was narrow and relatively uniform, and the means of hybrids fell between the means of the two parental lines.

SUMMARY

A progeny test of two inbred strains of Solo papaya, Line 8 and Line 9, and their reciprocal hybrids was conducted in 1960 to determine the mode of inheritance of the characters terminal height, stem diameter, height to first flower, number of nodes to first flower, internode

length and earliness of flowering. The main objective was to search for sex-linked vegetative characters which might be useful in the separation of female and hermaphrodite plants at an early seedling stage. Significant differences could not however be detected between plants of different sexes.

For each character studied, pertinent statistics and analysis of variance were calculated. Means and frequency histograms were employed as a basis for setting up hypotheses concerning the mode of inheritance. The means of the hybrids were found to be intermediate and closely approaching the arithmetic means of the parental lines. None of the characters deviated significantly from the mid-point of the two parents, suggesting lack of dominance, and the possibility of the action of multiple factors with additive effects for characters studied.

Tests of mean differences were also made and it was found that the two parental lines differed significantly in all characters except stem diameter. Means of reciprocal hybrids failed to show significant differences at the 5 per cent level, suggesting that the inheritance involved was not cytoplasmic in nature, and that characters were not sex-linked.

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